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Carotenoid composition and photochemical activity of four sandy grassland species

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Abstract

The photosynthetic pigments and photochemical efficiency of photosystem 2 (PS2) were studied in four constitutive species (*Achillea millefolium* L., *Festuca pseudovina* Hack. *ex* Wiesb., *Potentilla arenaria* Borkh., and *Thymus degenianus* Lyka) of a semiarid grassland in South-eastern Hungary. Every species displayed typical sun-adapted traits and substantial plasticity in the composition and functioning of the photosynthetic apparatus. The contents of chlorophylls (Chls) and carotenoids (Cars) on a dry matter basis declined from May to July, however, the amount of total Cars on a Chl basis increased. This increase was the largest in *Potentilla* (48 %) and the smallest in *Achillea* (14 %). The pool of xanthophylls (VAZ) was between 25 % and 45 % of the total Car content and was larger in July than in May. The content of β-carotene increased by July, but lutein content did not change significantly. The Chl fluorescence ratio F_v/F_m was reduced by 3–10 % at noon, reflecting the down-regulation of PS2 in the period of high irradiance and high temperature. The occurrence of minimal values of $\Delta F/F_m'$ showed close correlation to the de-epoxidation rate of violaxanthin. Hence in natural habitats these species developed a considerable capacity to dissipate excess excitation energy in the summer period in their photosynthetic apparatus through the xanthophyll cycle pool and a related photoprotective mechanism, when the photochemical utilization of photon energy was down-regulated.

Additional key words: chlorophyll; dry mass; photochemical efficiency; photosystem 2; seasonal changes; species differences; xanthophyll cycle.

Introduction

Semiarid grasslands represent a peculiar vegetation type of the temperate zone where plants continuously have to cope with the effects of high irradiance and excess photons occurring alongside with high temperature and temporal water shortage in summer months. These communities are very sensitive to the effects of global climate change and the uncertainties of climate (Archer *et al.* 1995). Plants adapt to these extreme environments by a wide range of alterations in their morphology, anatomy, and physiology (Nagy *et al.* 1998, Gratani and Bombelli 1999). Most species occurring in these habitats are typically drought tolerant monocots or dicots with reduced shoots and thick leaves, more or less considered as xerophytes. Beside the specific morphology due to the regulation of water balance, they developed mechanisms for protection against the harmful effects of excess absorbed photons at the level of both their leaf surfaces and chloroplasts so that the most efficient CO_2 assimilation could be performed (Kalapos 1994, Nagy *et al.* 1994, Tuba *et al.* 1996, Veres *et al.* 2001).

There is a bulk of information on the involvement of carotenoids (Cars) in the stress tolerance of plants that suggests a very close relationship between the functioning and conditions of the photosynthetic apparatus and its pigment composition (Young 1991, Demmig-Adams and Adams 1992). They perform a variety of crucial functions. Cars are integral components of the photosynthetic apparatus (Humbeck *et al.* 1989). They are light-harvesting pigments, can deactivate the excited triplet state of chlorophyll (Chl) (Sieferman-Harms 1987, Young 1991), also have a photoprotective function. The Car content and composition can be affected by several environmental factors, and show a great interspecific variation (Demmig-Adams and Adams 1996).

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Abbreviations: Car: carotenoid; Chl: chlorophyll; DEPS: de-epoxidation index; DM: dry matter; F_v/F_m: potential photochemical efficiency of photosystem 2; $\Delta F/F_m'$: actual photochemical efficiency of PS2; FM: fresh matter; PFD: photon flux density; PS2: photosystem 2; VAZ: violaxanthin (V) + antheraxanthin (A) + zeaxanthin (Z).

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When plants are exposed to high irradiance surpassing the extent that can be utilized in photosynthetic electron transport, non-photochemical dissipation of excitation energy is induced as a mechanism for photoprotection of photosystem 2 (PS2) (Park *et al.* 1995). The energy dissipation takes place in correlation with the accumulation of zeaxanthin (Z) in the xanthophyll cycle (Sapozhnikov *et al.* 1957, Yamamoto *et al.* 1962). The de-epoxy components of the xanthophyll cycle have a crucial role in the de-excitation of Chl, when irradiance is excessive (Demmig-Adams and Adams 1992, Adams and Demmig-Adams 1995, Niyogi *et al.* 1997).

The avoidance of harmful effects of photoinhibition and photodamage should inherently be accompanied with the plastic responses of Cars to the fluctuations of irradiance in natural environments (Björkman and Demmig-Adams 1994). In plant communities like grasslands, where the vegetation structure allows full penetration of photons to the soil surface, all species show typical sun-adapted physiology and photoprotection, but they can also experience excess photons as depending on the extent of constraints from other abiotic factors. In semiarid habitats, high irradiance frequently occurs in the combination of high temperature and temporary drought. Thus, considering that summer periods are critical for the growth and photosynthetic performance of plants in these habitats, we investigated seasonal changes in the Car composition, and the relationship between the photochemical efficiency of PS2 and the photoprotective xanthophyll cycle of dominant species of a natural semiarid grassland in a sandy area in SE-Hungary.

Materials and methods

Plants, experimental site, and meterological data: The experimental site is situated in the Hungarian Great Plain (South-East of Hungary) at 150 m above the sea level. The soil of the area is slightly acidic sandy soil, the climate is temperate-continental with hot dry summers: the mean annual rainfall is 500 mm or less, the mean annual temperature is 11 °C (Précsényi and Mészáros 1997). The investigations were performed in the sampling periods 15–17 May and 15–17 July during the growing season of 1997. This growing season was moderately hot and there was no serious drought. The average daily temperature ranged from 7 (April) to 21 (July) °C and the total rainfall was 278 mm (63 % of the yearly amount) in the vegetation period. July was the warmest month when the daily maximum temperature was often above 30 °C (Fig. 1). Rainfall and temperature data were obtained from the meteorological station of Debrecen University (SE-Hungary), which is situated near the experimental site. The experimental site is covered with a type of xerotherm grasslands described as Potentillo-Festucetum pseudovinae community as concerns floristic composition. The plant coverage of the site is 70–80 %. Four constitutive species making up 60 % of the total biomass of the stand were *Achillea millefolium* L., *Festuca pseudovina* Hack. *ex* Wiesb., *Potentilla arenaria* Borkh., and *Thymus degenianus* Lyka (Veres *et al.* 2000). *F. pseudovina*, the dominant monocot species of the grassland has sclerenchymatic erect leaves with a waxy surface. The other three species are dicots, and exhibit certain variations in the morphology of the leaf blade and leaf surface: *P. arenaria* has soft and composed leaves with trichomes appearing very densely on the abaxial surface. *T. degenianus* has small leaves with trichomes, but *A. millefolium* has soft and strongly incised leaves. All the species are perennials and have a C_3 photosynthetic pathway.

Diurnal changes in air temperature and photon flux density (PFD) were recorded at the top of the grassland canopy during the measurements (Fig. 1) with the quantum and temperature sensor of *PAM-2000* fluorometer (*Walz*, Germany). The maximal value of PFD was around 1 600 and 1 800 µmol m^{-2} s^{-1} on the days of measurements. At dawn, the temperature was around 10 °C in May and 15 °C in July. The maximal air temperature was 33–35 °C in May and 40–42 °C in July.

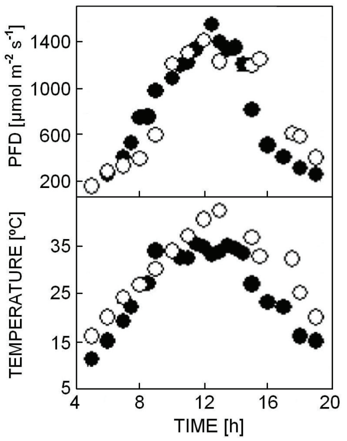

Fig. 1. Diurnal changes of photon flux density (PFD) [µmol m^{-2} s^{-1}] and air temperature [°C] on 15 May (●) and 17 July (○) measured at the surface of vegetation.

Chl fluorescence: The potential photochemical efficiency of PS2 (F_v/F_m) and the daily course of the actual photochemical efficiency of PS2 [$(F_m' - F_t)/F_m' = \Delta F/F_m'$] were detected by means of *PAM 2000* modulated light fluorometer (*Walz*, Germany), and calculated as suggested by Genty *et al.* (1989). In both sampling periods, F_v/F_m was measured at dawn (5–6 h) and at noon (13–14 h) after a 30 min dark adaptation period. $\Delta F/F_m'$ was continuously determined during the day under natural irradiation. F_v/F_m values were measured in leaves after dark adaptation in special leaf clips. The diurnal course of $\Delta F/F_m$' was measured on the same plants. At each sampling time, six measurements were made on leaves of randomly chosen plants. The examined plants were of similar age.

Photosynthetic pigments: As parallel to Chl fluorescence measurements, leaf samples were collected for analyzing photosynthetic pigments. Leaf segments were cut from the plants and immediately wrapped in aluminium foil, dropped in liquid nitrogen, and stored in it until processing. Samples were powdered in liquid nitrogen and pigments were extracted with 80 % acetone (with 0.1 % NH_4OH) at 4 °C. The absorbance of extracts was measured at 470.0, 663.2, and 646.8 nm with spectrophotometer UV/VIS *1601* (*Shimadzu*, Japan). These absorbance values were used for calculation of Chl *a*, Chl *b*, and total Car contents by means of formulae suggested by Wellburn (1994). The Car components were determined in the same extract by the HPLC method (Goodwin and Britton 1988) using a *Nucleosil C18* column. The eluents were acetonitril and water (9 : 1 with 0.01 % triethylamine) and ethylacetate (HPLC-system equipped with an UV/VIS detector, *JASCO*, Japan). Z was regularly injected as a standard compound during the analyses for the identification of peaks in the chromatogram and calculation of pigment contents (Tóth *et al.* 2002).

Dry matter (DM): The fresh matter/dry matter ratio (FM/DM) of leaves (200–250 mg) was measured as parallel to the pigment analysis. After FM was determined, the plant material was dried at 85 °C in an oven, and DM was measured after 48 h.

Statistical analysis: Student *t*-test and one-way ANOVA were applied by means of *Microsoft® Excel 2000*, *SigmaPlot 2001 7.0*, and *SPSS 11.0*.

Results and discussion

Leaf pigment composition: A wide range of species in the semiarid grasslands in Hungary can be described by relatively high Car contents as a constitutive trait of their environmental tolerance (Tuba 1984, Mészáros *et al.* 1996, Veres *et al.* 2000). The contents of Cars and Chls on a DM basis showed a decline in the leaves of the four species by summer (Fig. 2). As concerns leaf Chl contents per DM, all the species displayed significant 30–40 % decreases from May to July (except for *Festuca*, where the changes were not significant). Different biochemical, morphological, and/or anatomical characteristics may influence the reduction of Chl content (Murthy and Rajagopal 1995). Thus in *Fetuca*, paraheliotropic leaves may have a specific role in avoiding high irradiance. The decrease in Chl content per unit DM from May to July might be due to the relative increase in the

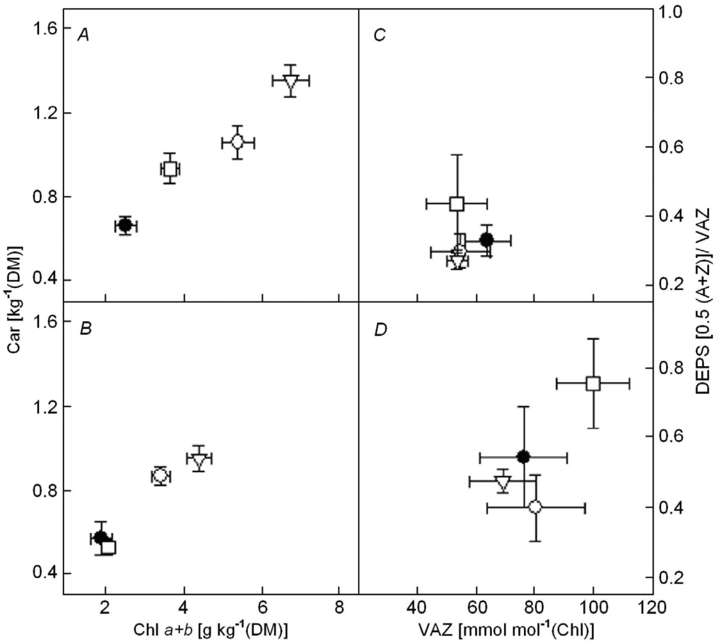

Fig. 2. Chlorophyll (Chl) *a*+*b* and total carotenoid (Car) contents on dry matter basis (*A, B*) and relationship between the de-epoxidation state of the xanthophyll cycle and the content of violaxanthin + antheraxanthin + zeaxanthin (VAZ) on Chl basis (*C, D*) of *Festuca pseudovina* (●), *Potentilla arenaria* (□), *Thymus degenianus* (○), and *Achillea millefolium* (□) on 15 May (*A, C*) and in 17 July (*B, D*). Means of 4–6 replicates ± S.E. Significant seasonal changes in Chl (a) and Car (b) contents were as follows: *Potentilla*: ab, *Thymus*: a, *Achillea*: ab. Significant changes in DEPS (c) and VAZ (d) in *C* and *D* were as follows: *Festuca*: d, *Potentilla*: d, *Thymus*: d.

DM of the leaves: from May to July DM of leaves increased by 25–30 % (data not shown). The differences between the changes in DM and Chl contents indicate a 10–15 % degradation of the pigments. Beside the DM accumulation the senescence processes might also contribute to the Chl reduction (Munné-Bosch and Alegre 2004). The leaf senescence is usually enhanced by several abiotic stress factors under field conditions, such as drought, high temperature, high irradiance, and UV-radiation (Pjon 1981, De Luca d'Oro and Trippi 1987, Joshi *et al.* 1991, Mészáros *et al.* 2001). The lesser Chl content means a reduction in the amount of photons absorbed by leaves, and requires higher capacity to dissipate excess excitation energy per PFD absorbed (Munné-Bosch and Alegre 2000b).

The Car content was the lowest [0.45–0.62 g kg^{-1} (DM)] and the most stable in the monocot species (*Festuca*) during the season. From the group of dicot species, *Potentilla* had the lowest and *Achillea* the highest content of total Cars. The decline in the Car content was much slighter in the leaves of *Festuca* and *Thymus*, it amounted to 15–20 %, while it was 30–45 % in *Potentilla* and *Achillea* by July ($p<0.01$). Chl and Car contents were significantly different among individual species in the measurement period ($p<0.001$). Similar or higher extents of summer reduction in the leaf Chl were reported for the xerophyte species of semiarid grasslands and Mediterranean sites (Tuba 1984, Munné-Bosch and Alegre 2000a, Ain-Lhout *et al.* 2004). The contents of Chls and Cars on a DM basis declined from May to July, however, the amount of total Cars on a Chl basis increased.

Lutein was the most abundant Car in every species (Table 1). This pigment also may have a crucial role in protecting the photosynthetic apparatus (Pogson *et al.* 1996, Niyogi *et al.* 1997, Gilmore and Ball 2000). The lutein content varied between 70 and 140 mmol mol^{-1}(Chl) in all the observed species. No significant changes occurred in the content of lutein by July, and there were no significant differences among the species. Lutein has a crucial role in the structures of light-harvesting complex (Sieferman-Harms 1985), thus its unchanged status indicates that the actual environmental conditions did not result in serious degradation. In *Potentilla* and *Thymus*, the β-carotene content exhibited a 70 % increase during the summer, while in the leaves of *Festuca* and *Achillea* no significant increases could be observed from May to July (Table 1). Tuba (1984) also detected higher β-carotene content in a similar habitat by summer following the drought stress. Neoxanthin content did not change significantly by July (Table 1), similarly to findings of Demmig-Adams and Adams (1996) and Eskling and Akerlund (1998). As opposed to this fact, Munné-Bosch and Alegre (2000a) found in field-grown *Lavandula stoechas* that the content of neoxanthin increased by 50 % during summer, and they attributed this observation to the effects of progressive drought causing leaf dehydration. In the leaf pigment extract, lutein-5,6-diepoxide and β-carotene are also often found as minor components (Bungard *et al.* 1999, Matsuhara *et al.* 2001). These pigments were not detected in leaves of the four species.

Pigments involved in the xanthophyll cycle respond the most sensitively to the presence of excess photons. All the species had a relatively large xanthophyll pool (Table 1) in contrast to mesophyte species (Mészáros *et al.* 1996). This phenomenon is a result of long-term adaptation to the environment as shown for other sun plants (Logan *et al.* 1996). In May, the xanthophyll cycle pool was the largest for *Festuca* [56±1 mmol mol^{-1}(Chl)]. In contrast, the other three broad-leaf species had relatively smaller VAZ pool [43–54 mmol mol^{-1}(Chl)]. In May, there were no significant differences among species in the contents of xanthophyll cycle pigments, although in July significant differences were observed. Generally, our species had larger VAZ pool in July (30–60 % increase) with the exception of *Achillea*; this species did not show significant seasonal variation in its VAZ pool. Increases in the VAZ pool under high irradiance may be generated by a stimulated *de novo* Z synthesis from β-carotene (Schindler and Lichtenthaler 1996). This study partly supports this hypothesis, since the largest enhancement of VAZ pool was found for *Potentilla* (60 %), and the β-carotene content also showed a large increase (70 %) in leaves of *Potentilla* by July (Table 1).

Relationship between photochemical activity and VAZ cycle pool: F_v/F_m significantly decreased by noon in all the species except for *Thymus*, but the differences between the May and July results were not emphatic (Table 2). The midday decline in PS2 optimal photochemical efficiency indicated the down-regulation of the primary reactions in photosynthesis as a photoprotective response (Somersalo and Krause 1989). Under field conditions, it is a frequently appearing phenomenon that primarily results from the enhanced activity of the xanthophyll cycle connected to the thermal dissipation of excitation energy (Demmig-Adams *et al.* 1992). When *in vivo* Chl fluorescence measurements were carried out, it was not possible to distinguish between the two main causes of down-regulation of the potential photochemical activity, since the actual value of ground fluorescence is generally the result of the co-occurring photoprotection and photoinactivation (Osmond 1994). In whatever proportions these processes induced the decline of F_v/F_m in our species, it appeared in correlation with the conversion rate of V to Z and A de-epoxidation. The de-epoxidation index (DEPS) reflecting the extent of this process in relation to the total VAZ cycle pool increased from May to July (Fig. 2*C,D*). Considering the climatic data, the sampling periods were not severe, but higher temperature extremes occurred in July. This might contribute to the increase of DEPS and the VAZ cycle pool by July indicating a larger need for the dissipation of excitation energy in the photosynthetic apparatus. The

Table 1. Changes in carotenoid contents [mmol mol^{-1}(Chl)] in four grassland species at noon (13–14 h) of 15 May and of 17 July in 1997. Means ± S.E. $n = 4$–6. $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

		Neoxanthin	V+A+Z	Lutein	β-carotene
May	*Festuca*	16.29 ± 1.3	56.16 ± 1.0	117.07 ± 0.1	33.41 ± 7.2
	Potentilla	10.92 ± 0.7	43.21 ± 1.1	72.58 ± 4.2	13.09 ± 0.9
	Thymus	15.01 ± 1.9	54.55 ± 0.1	99.14 ± 9.3	15.09 ± 1.0
	Achillea	16.47 ± 1.8	53.68 ± 3.4	101.61 ± 10.3	20.99 ± 1.7
July	*Festuca*	15.79 ± 1.6	$88.05 \pm 14.3^{**}$	140.62 ± 11.7	29.07 ± 1.6
	Potentilla	14.27 ± 3.8	$99.98 \pm 15.1^{**}$	109.21 ± 11.9	$45.48 \pm 2.1^{***}$
	Thymus	16.84 ± 1.2	$80.27 \pm 16.7^{*}$	114.41 ± 19.3	$50.88 \pm 1.3^{**}$
	Achillea	17.82 ± 1.9	69.11 ± 5.8	104.23 ± 12.1	33.21 ± 3.1

Table 2. Changes in the potential photochemical activity (F_v/F_m) in leaves of four grassland species at dawn (5–6 h) and at noon (13–14 h) on 15 May and 17 July of 1997. Means ± S.E. $n = 6$. Significant differences between dawn and noon: $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$. *Letters* indicate significant differences between the average daily values in May and July: a: $p<0.05$, b: no significant differences.

	May		July	
	at dawn	at noon	at dawn	at noon
Festuca	0.800 ± 0.003	$0.777 \pm 0.002^{****}$	0.781 ± 0.003 a	$0.748 \pm 0.010^{**}$ a
Potentilla	0.818 ± 0.002	$0.798 \pm 0.004^{****}$	0.822 ± 0.002 b	$0.783 \pm 0.003^{****}$ b
Thymus	0.825 ± 0.003	$0.734 \pm 0.023^{****}$	0.783 ± 0.011 a	0.776 ± 0.005 b
Achillea	0.821 ± 0.004	$0.792 \pm 0.010^{***}$	0.813 ± 0.001 b	$0.732 \pm 0.001^{***}$ b

DEPS index varied significantly among the species only in July ($p<0.001$). For *Potentilla* and *Festuca* the DEPS was higher than for the other two species both in May and July (Fig. 2*C,D*). In the leaves of *Thymus* DEPS was small, and *Achillea* had the least active xanthophyll cycle.

In leaves that developed under high irradiance, the size of the xanthophyll cycle pool can represent 30 % of the total Cars (Demmig-Adams and Adams 1992). We found that the size of the xanthophyll cycle pool of grassland species ranged 25–48 %, and showed a significant increase by July (Table 1, Fig. 2*C,D*). The seasonal differences in the DEPS also showed that the de-epoxidation of V to Z took place very partially in May. The two de-epoxy components were present in similar amounts, and in July Z became the dominant component (data not shown). The variation in the diurnal courses of the formation of the two de-epoxy components of the VAZ cycle with the changes of environmental stress and senescence were reported for other plants grown in field (Young 1991, Demmig-Adams and Adams 1992). The two- and three-fold increase of the Z content by July also reflected the increasing need for the dissipation of excess photons and the reduction of CO_2-assimilation.

The actual photochemical efficiency of PS2 changed (Fig. 3) in a close inverse correlation with PFD during the day (Fig. 1). Values of $\Delta F/F_m'$ showed diurnal transient decreases around noon in all the species (Fig. 3), which is a general feature of photosynthesis in natural environments (Demmig-Adams and Adams 1992) connected with down-regulation in light (Krause and Weis 1991). In *Festuca* and *Potentilla*, the minimal values of $\Delta F/F_m'$ at noon were low, they ranged between 0.1 and 0.2, indicating a strong over-reduction of PS2. In *Thymus* and especially in *Achillea*, the minimal $\Delta F/F_m'$ was higher (0.2–0.4). The values of $\Delta F/F_m'$ in *Festuca* and *Potentilla* indicate that these species were more susceptible to photoinhibition during the study period than *Thymus* and *Achillea*. In these latter species, leaf properties may also play a specific role in avoiding the effects of high temperature, high irradiance, and leaf dehydration. The

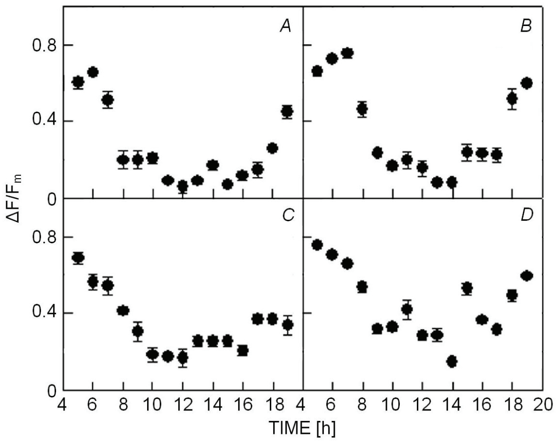

Fig. 3. Diurnal time courses of actual photochemical activity [$\Delta F/F_m' = (F_m' - F_t)/F_m'$] of four dominant grassland species were measured on 17 July from dawn to evening. Investigations were performed parallel with sampling for pigment analysis in *Festuca pseudovina* (*A*), *Potentilla arenaria* (*B*), *Thymus degenianus* (*C*), and *Achillea millefolium* (*D*). Means of six replicates ± S.E.

mophology and anatomy of these species can contribute to this phenomenon. Valladares *et al.* (1997) also observed a strong decline in the $\Delta F/F_m$' in drought tolerant chaparral species (*Heteromeles arbutifolia*) under multiple co-occurring stresses in summer. The daily minimal values of $\Delta F/F_m$' were in close correlation to the de-epoxidation of V (Fig. 2*C,D*). When low values occur for $\Delta F/F_m$', the dissipation of excess energy through various non-photo-chemical processes involving Z formation becomes crucial for the avoidance of the photodamages to PS2.

In conclusion, our results show that the plants grown under the extreme environment of the semiarid habitat do not only have special morphological adaptations, but their physiology acclimates to the short-term and long-term fluctuations of environmental conditions. These drought tolerant, xerophyte species exhibit great Car contents and xanthophyll cycle pool for dissipating excess excitation energy of the photosynthetic apparatus and maintaining the recovery of photochemical efficiency.

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